Revue suisse de Zoologie, vol. hors série: 135-140; août 1996

Variation in burrow morphology of Mediterranean trapdoor spiders (Ctenizidae, Cyrtaucheniidae, Nemesiidae)

Arthur E. DECAE
National Museum of Natural History
NL-2311 PL Leiden, The Netherlands.

Variation in burrow morphology of Mediterranean trapdoor spiders (Ctenizidae, Cyrtaucheniidae, Nemesiidae). - Trapdoor spiders in the European Mediterranean often occur in assemblages of two or more congeneric species. Conspicuously the burrow structure always differs qualitatively between the species in such syntopic congeneric complexes.
It is suggested here that quantitative differences in burrow structure (such as depth of the burrow tube, thickness of the trapdoor, extent of the silk lining) are generally explicable as adaptations to the physical habitat, whereas qualitative differences (such as the presence or absence of branching tubes, internal plugs or socks, rim ornamentation) more likely result from interspecific interactions.

Key-words: burrow variation - trapdoor spiders - Mediterranean - syntopic - habitat specific - interspecific interaction.

INTRODUCTION

Trapdoor spiders build a wide array of different types of burrows (Figs 1 & 2). The structure of the trapdoor itself varies from a thin flexible silken flap (waferdoor) to a thick bathplug-like device (corkdoor). The trapdoor may be absent altogether, it may take the form of a rigid collar or there may be two trapdoors to one burrow. The burrow rim may be furnished with radiating silk lines, organized linear litter fans (Fig. 3) or haphazardly spun-in debris, it may be devoid of any of these things, expanded beyond the edges of the trapdoor or only just reaching the soil surface. The burrow tubes vary greatly in length and in shape. There may be special escape tunnels or dead ended side tubes. Generally the burrows are dug into the ground, but they may also be constructed above the ground, in logs or on the trunks of trees. There may be one or

Manuscript accepted 25.10.1995.
Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8.IX.1995

more internal doors, movable or fixed plugs, internal silken socks and furthermore there may be variation in the extent and structure of the silk lining and burrow plastering.

Notwithstanding the great variation in trapdoor burrow design, only a few basic, qualitatively different burrow types are recognized. The informal classification of basic burrow types still rests on MOGGRIDGE's (1873, 1874) observations. Since Moggridge, students of trapdoor spiders informally distinguish cork-burrows from wafer-burrows on grounds of the structure, shape and fitting of the trapdoor, simple burrows from branched burrows based on the presence or absence of side tubes, and complex burrows on grounds of the presence of internal doors, socks, plugs or other devices.

It is important to realize that MOGGRIDGE's (1873, 1874) classification of trapdoor burrows was almost solely based on observations he made on a few species of the

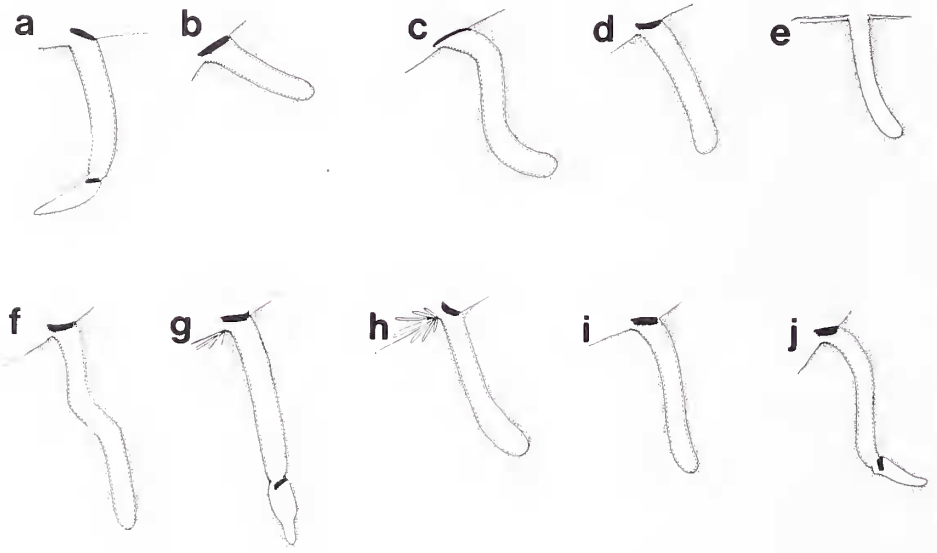

FIG. 1

Schematic representations of European Mediterranean trapdoor burrows. The doors are illustrated in solid black and in the unnatural position of being opened. Dashed lines represent the silk linings of the burrows. All burrows are drawn after observations made by the author unless stated otherwise. A) *Ummidia piceus* (after BACELAR 1933); B) *Ummidia* sp., near Grazalema (S. Spain); C) *Cyrtauchenius similis* (after BUCHLI 1966); D) *Cteniza moggridgei* (after MOGGRIDGE 1873); E) *Brachythele denieri*, near Tripolis (Peloponnissos); F) *Cyrtocarenum cunicularium*, Nauplion (Peloponnissos); G) *C. cunicularium*, Sakynthos (Ionian islands); H) *C. cunicularium*, near Chania (W. Crete); I) *C. grajum*, Sakynthos (Ionian islands); J) *C. grajum*, near Gythion (Peloponnissos).

genus Nemesia he studied in Southern France. His burrow classification system nevertheless is broadly applicable to describe the nests of trapdoor spiders in all families and from all over the world.

This is interesting in the light of searching for the factors that influence burrow design, because it appears that non-related, or only distantly related species, may build virtually identical burrows, while closely related species often build distinctly different types of burrows. Generally speaking however burrow design is species specific and it has been used in taxonomical classification (e.g SIMON 1914, COYLE 1994). Nevertheless, even at the species' level burrow structure may vary qualitatively as will be shown. Possible factors that influence burrow design in trapdoor spiders are discussed.

HABITAT SPECIFIC BURROWS

If burrow construction behaviour in trapdoor spiders is genetically flexible, as indicated above, it might largely be determined by environmental conditions. In other words: do particular burrow-forms typically occur in particular habitats (or micro-habitats)?

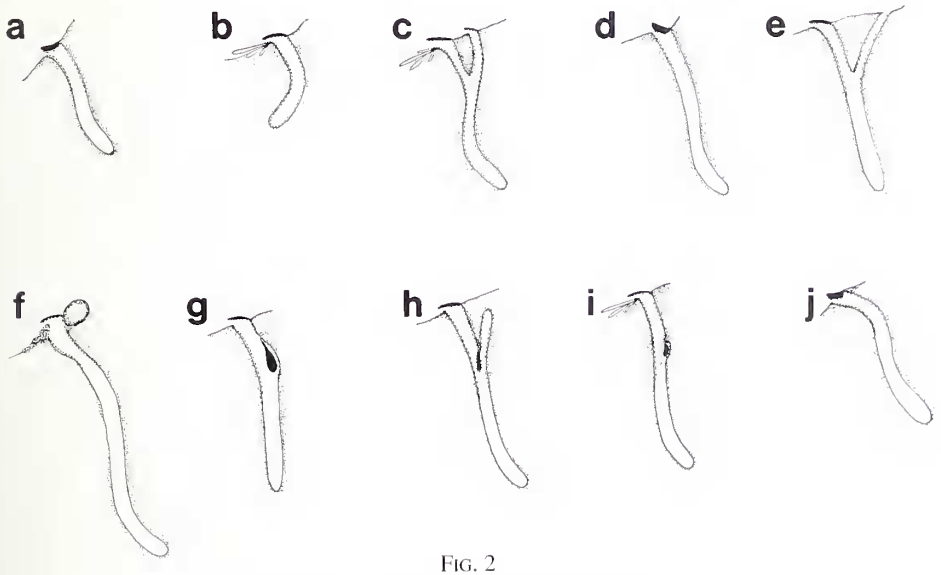

FIG. 2

Schematic representations of European Mediterranean trapdoor burrows (see also Fig. 1) in the genus *Nemesia*. A), B) & C) burrows of three different *Nemesia* species found in one roadside bank near Nerja (S. Spain, prov. Málaga); D) & E) *N. caementaria* and *N. dubia* found syntopically near Clapiers (Montpellier); F) *N. simoni* (Corbières); G) *N. fagei* (after BACELAR 1933); H), I) & J) *N. mandersjernae*, *N. congener* and *N. carminans* found syntopically near Cavalaire (Provence).

In an earlier presentation (DECAE 1993) I have strongly argued in favour of this view. I have said that I found burrows in open and exposed habitats to be generally deeper and have thicker and more tightly fitting trapdoors than burrows found in more shady, humid or forest habitats. COYLE & ICENOGLE (1994) suggest for species of the genus *Aliatypus* that burrow depth is directly related to aridity of the habitat in which the burrows are found. MAIN (1976) states for the genus *Aganippe* that she found "a whole array of related forms each with its own distinctive type of burrow which occurred in a distinctive sort of habitat." Understanding the habitat relations of particular burrow types depends on understanding the functions of the various structures involved (different surface doors, various forms of burrow rim ornamentation, branching tubes, internal doors, socks, plugs, etc.). COYLE & ICENOGLE (1994) give a number of valuable suggestions, but obviously still much has to be learned. Broadly speaking however, students of orthognathe spiders currently seem to agree that the burrowing habit and most burrow characters essentially have defensive functions: firstly, as an escape from adverse conditions related to the physical habitat, secondly as a defence against predators and parasites (COYLE & ICENOGLE 1994; DECAE 1993; MAIN 1993). Observations on the European Mediterranean trapdoor spider fauna however suggest that habitat related burrow variation is generally quantitative in nature (deeper burrows, thicker doors etc.) and that qualitative variation in burrow structure probably results from various competitive interactions.

SYNTOPIC COMMUNITIES AND INTERSPECIFIC INTERACTION

A common phenomenon in trapdoor spider communities all over the world is the syntopic aggregation of different species. Generally the members of such assemblages are not closely related (MAIN 1976; COYLE & ICENOGLE 1994). In the North Western Mediterranean however mixed aggregations of two or more *Nemesia* species are found in many places. Conspicuously the burrows of the congeneric members of such assemblies are always qualitatively distinct. Typically syntopical communities of two or more *Nemesia* species contain one species that constructs an unbranched cork burrow and another species that builds a more or less complex branched wafer burrow (Fig 2).

It is suggested here that high competitive pressure in syntopic congeneric species may have a dual effect of both sharpening and diversifying the dominant features of these species' common life strategy. In other words, if defence against physical and biotic hazards is the prime feature in the life strategy of trapdoor spiders, strong interspecific competition may improve the defensive qualities of two syntopic congeneric species in different directions, enlarging the phenotypic gap between the co-existing burrow types. Both the development of a corkdoor and the origin of branched burrow tubes in *Nemesia* are thus seen as defensive specialisations of an ancestral unbranched wafer burrow as found in *N. simoni* Cambr. (Fig. 2-F), a species not known to occur syntopically with other trapdoor spiders.

A more puzzling phenomenom related to what is discussed, was found in the genus *Cyrtocarenum* in Greece. The genus *Cyrtocarenum* contains two species, *C.*

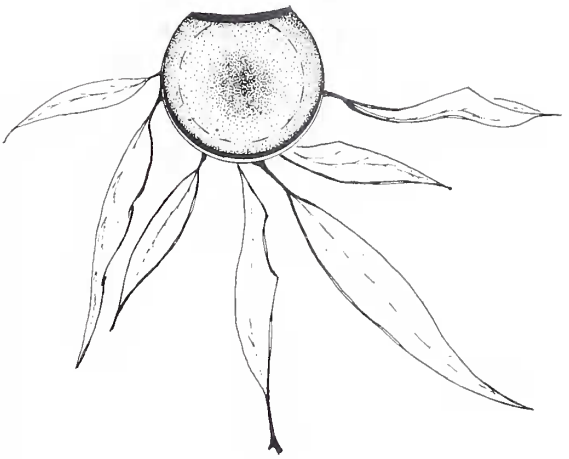

FIG. 3

Burrow entrance of *Cyrtocarenum cunicularium* from Western Crete, showing a well organized litter fan of olive leaves.

cunicularium (Olivier) and *C. grajum* (C. L. Koch) (DECAE 1996). On the Ionian island of Sakynthos (and other Ionian islands) the two species occur in mixed populations, digging their burrows only centimeters apart. In these colonies the burrow structure of adult females of the two species differ qualitatively. Saunders (1842) for the first time described the enigmatic inverted corkdoor (Fig. 1-G) found at the bottom of the burrow of Ionian trapdoor spiders. My observations on Sakynthos showed that *C. cunicularium* is the species that constructs this strangely inverted trapdoor. *C. grajum* in the mixed populations on Sakynthos builds the usual "simple type cork burrow" (Fig. 1-I). Research on the nearby Peloponnissos, where both species occur parapatrically (DECAE 1996) resulted in the observation that the situation was reversed. Here *C. grajum* (Fig. 1-J) makes the inverted bottom door, while *C. cunicularium* (Fig. 1-F) constructs a classical simple cork door burrow. To make the confusion complete, it was found that on Crete (were *C. grajum* is presumably absent and *C. cunicularium* locally occurs syntopically with a *Nemesia* species that constructs a branched waferdoor burrow), *C. cunicularium* in the eastern part of the island builds the inverted corkdoor, while this same species in central Crete builds a common simple cork burrow and in western Crete provides the entrance rim of her burrow with a most magnificent litter fan that was found nowhere else (Fig. 3).

CONCLUSION

Observations on the European Mediterranean trapdoor spider fauna show that qualitatively different burrow types particularly occur in mixed aggregations of congeneric species. This observation suggests that interspecific interaction represents

an important factor in the origin of qualitatively different burrow structures found in the region. It is realized that the cases presented here are little more than local field observations and that the hypothesis of competitive interaction as a cause for the origin of qualitative differences in burrow structure is not more than a first idea. No doubt alternative explanations are possible and observations elsewhere may contradict the situation in the Mediterranean. However, it is believed that the phenomena described are open to research and that the observations and thoughts presented here can serve as a basis for discussion and further work aimed at illuminating the factors that determine trapdoor burrow structure.

REFERENCES

Bacelar, A. 1933. Sur les moeurs des *Nemesia* et des *Pachylomerus*. *Bulletin de la Société Portugaise des Sciences Naturelles* 9 (27): 291-295.

Buchli, H.H.R. 1966. Notes sur la Mygale terricole *Amblyocarenum simile* (Ausserer, 1871) Arachnida, Araneae). *Senckenbergiana Biologica* 47 (1): 11-22.

Coyle, F.A. 1994. Analysis of the Trapdoor Spider Genus *Aliatypus* (Araneae, Anthrodiaetidae). *The Journal of Arachnology* 22: 218-224.

Coyle, F.A. & Icenogle, W.R. 1994. Natural History of the Californian Trapdoor Spider Genus *Aliatypus* (Araneae, Anthrodiaetidae). *The Journal of Arachnology* 22: 225-255.

Decae, A.E. 1993. The trapdoor-burrow: the success of a defensive system. *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 116-1: 287-292.

Decae, A.E. 1996. Systematics of the Trapdoor Spider Genus *Cyrtocarenum* Ausserer, 1871 (Araneae, Ctenizidae). *Bulletin of the British Arachnological Society.*

Main, B.Y. 1976. Spiders. *The Australian Naturalist Library. Collins Sydney-London:* 80.

Main, B.Y. 1993. From Flood Avoidance to Foraging: Adaptive Shifts in Trapdoor Spider Behaviour. *Memoirs of the Queensland Museum* 33(2): 599-606.

Moggridge, J.T. 1873. Harvesting Ants and Trapdoor Spiders. *L. Reeve, London*: 73-151.

Moggridge, J.T. 1874. A Supplement to Harvesting Ants and Trapdoor Spiders. *L. Reeve, London:* 180-301.

Saunders, S.S. 1842. Description of a Species of Mygale, from Ionia, with its Nest. *Transactions of the Entomological Society London* 3:165-170.

Simon, E. 1914. *Les Arachnides de France*. 6(1): 1-21.